Applied Soil Ecology 120 (2017) 70–80

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Mechanism of biocrusts boosting and utilizing non-rainfall water in Hobq Desert of China

Hailong Ouyang[a,b], Shubin Lan[a], Haijian Yang[a], Chunxiang Hu[a,*]

[a] Key Laboratory of Algal Biology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Keywords:
Non-rainfall water
Accumulation patterns
Sources
Influencing factors
Photosynthetic activities
CO_2 exchange

ABSTRACT

Non-rainfall water (NRW), as the most frequent water source of drylands, is significantly boosted by biocrusts. However, the mechanism of biocrustal promotion and utilization of NRW have been little studied. In this paper, the NRW accumulation patterns, photosynthetic activities and CO_2 exchange of different biocrusts (2 cyanobacteria crusts-ACs, 1 cyanolichen crust-LC1, 1 green algae lichen crust-LC2, and 1 moss crust-MC) under NRW were studied through in situ mesocosm experiments in the Hobq Desert of China during the autumns of 2014 and 2015. Structural equation models showed that crustal properties feedback affected the degree of meteorological parameters on NRW accumulation, in which the effect of surface temperature gradually decreased with the development of biocrusts while that of subsoil temperature and light intensity increased. As for the sources, ca. 50% of NRW in ACs derived from subsoil but more than 78% from atmosphere in LCs and MC, and this pattern was obviously influenced by the recovery degree of photosynthetic activity. But the diel maximum NRW (NRW_{max}) were mainly determined by crust thickness, photoautotroph biomass and other properties. During NRW accumulation, the recovery of photosynthetic activity in ACs was the earliest, followed by that of LC2 and MC, LC1 never recovered. Whereas, the initial CO_2 exchange of ACs and MC were often earlier than that of LC2, and the minimum diel NRW_{max} required by ACs, LC2, and MC to maintain carbon balance were ca. 0.08, 0.17, and 0.20 mm, respectively. Thus we proposed the application boundary of inoculation-based technology in drylands is the areas where the diel NRW_{max} exceed or equal 0.08 mm and carbon input under NRW last more than 2 h during NRW-abundant seasons.

1. Introduction

Easily peeled-off biocrusts, firstly colonized and stabilized by cyanobacteria, occupy more than 70% of the living coverage in arid and semi-arid areas, and make important contributions to the stabilization, fertilization, and hydrological regulation of topsoil (Belnap and Lange, 2001; Hu et al., 2002, 2012; Lan et al., 2014). Thus, fixing sandy surface utilizing biocrust is unquestionably a sustainable technology with broad application prospects (Bowker, 2007) and advantages (Hu et al., 2012; Lan et al., 2014; Zhao et al., 2016). This technology has been successfully applied in more than 40 km^2 desert region (Hu et al., 2012; Liu et al., 2013; Lan et al., 2014; Zhao et al., 2016). The technology is also being largely attempted and further extended globally (Zheng et al., 2011; Liu et al., 2013; Wu et al., 2013b; Xiao et al., 2015; Chiquoine et al., 2016; Mallen-Cooper and Eldridge, 2016). The cyanobacterial-based inoculation technology (inoculation-based technology for short) was applied according to the following experimental flow: (1) suitable strains are selected; (2) a stable mass-cultivation system for growing the selected strains is optimized; (3) a proper culture-dispersal strategy is chosen and optimized; (4) proper techniques for habitat ameliorations were chosen (Liu et al., 2013; Rossi et al., 2017).

Anyway water is the first limiting factor of lives, especially in drylands. The formation and development of biocrusts also need water, though the amount is much less than that required by vascular plants. In particular, they can utilize additional water sources, such as non-rainfall water (NRW). This kind of water can rarely be used by other organisms, but occurs about 200 nights per year in the northern Negev (Evenari et al., 1971). NRW comprises a great proportion of the total annual precipitation (Malek et al., 1999; Wang et al., 2014), even is the only water source in some places (Westbeld et al., 2009; Kaseke et al., 2012). However, frequent small water that cannot activate carbon-fixation results in carbon consumption (Coe et al., 2012; Reed et al., 2012). So the effectiveness of NRW on biocrusts is of vital importance to determine the boundary of inoculation-based technology, in which the carbon gain particularly relates to NRW amount, duration and carbon-

* Corresponding author.
E-mail addresses: ouyang19890121@126.com (H. Ouyang), shblan@163.com (S. Lan), haijian0102@163.com (H. Yang), cxhu@ihb.ac.cn (C. Hu).

http://dx.doi.org/10.1016/j.apsoil.2017.07.024
Received 22 December 2016; Received in revised form 14 July 2017; Accepted 15 July 2017
Available online 14 August 2017
0929-1393/

fixation time-point.

The formation of NRW is affected by climatic factors and soil surface properties together (Kidron, 2000; Kidron and Temina, 2013; Wang et al., 2014). For example, more NRW forms in sunny days than that in cloudy days. Longer time of high relative humidity in nighttime and smaller difference between air and dew-point are both beneficial to higher NRW amount. Vapor pressure and atmospheric pressure can also affect NRW by driving capillary effect (Agama and Berliner, 2006; Lan et al., 2010). Meanwhile, the presence of biocrusts significantly promotes the accumulation of NRW (Liu et al., 2006; Zhang et al., 2009; Lan et al., 2010; Pan et al., 2010; Uclés et al., 2015), which is attributed to roughness, or soil texture (Zhang et al., 2009; Pan et al., 2010; Zhuang and Zhao, 2014), exopolysaccharides and salinity (Kosmas et al., 2001; Kidron et al., 2002; Heusinkveld et al., 2006; Chen et al., 2014; Colica et al., 2014; Wang et al., 2014). However, NRW derives from both atmosphere and soil (Agam and Berliner, 2006; Lan et al., 2010), and the latter contains moisture stems from vapor and capillarity. The portions from atmosphere and soil may be affected by different properties, and the accumulation pattern of NRW should be the balanced result of biocrust traits and microclimate. Whereas, how different biocrusts boost accumulation of NRW and how affect different parts of NRW are little known.

Photosynthetic activity of biocrust organisms can conveniently reflect the potential of NRW. Chlorolichen (lichen with certain algae of Chlorophyta as phycobiont) crusts from the Negev Desert were detected from 18:30 h at night, and the threshold for photosynthetic activity of biocrusts was regarded as 0.1 mm liquid water (Lange et al., 1992). But the carbon balance may still be negative due to the limited duration and inappropriate time-point, even activity recovered. Actually CO_2 exchange can reflect the effectiveness of NRW. Several studies have investigated saxicolous or arboreal lichens utilizing NRW in heavy fog desert (Lange et al., 2001; Lange, 2003). However, biocrustal CO_2 exchange was limited to indoor simulation (Jeffries et al., 1993; Huang et al., 2014), or to artificial rehydration (Zaady et al., 2000; Housman et al., 2006; Su et al., 2012, 2013), determination after rainfall (Li et al., 2012), and other conditions excluding NRW (Feng et al., 2014; Darrouzet-Nardi et al., 2015). Though field measurements about carbon exchange of biocrusts were carried out (Wilske et al., 2008, 2009), few studies about in situ CO_2 exchange of biocrusts using NRW have been conducted.

Therefore, in this study, four types of biocrusts (two cyanobacteria crusts − ACs, one cyanolichen crust − LC1, one chlorolichen crust − LC2, and one moss crust − MC) that possess different carbon assimilation characteristics were selected, and the following work was in turn accomplished by in situ mesocosm experiments in the Hobq Desert (China). (1) The NRW amount and its proportions from atmosphere and soil were investigated during NRW-abundant seasons. (2) The crucial climatic factors and biocrustal properties affecting NRW accumulation were evaluated by multiple regression analysis. (3) The accumulation feedback pattern of NRW was analyzed and validated by structural equation model (SEM). (4) Photosynthetic activities and CO_2 exchange pattern of biocrusts under NRW were simultaneously in situ measured and analyzed. (5) The lowest diel maximum NRW of maintaining carbon balance was estimated.

2. Materials and methods

2.1. Experimental regions and sampling

The study was conducted in the Microalgae Experiment Station located in Dalate Banner of Inner Mongolia Autonomous Region, at the east edge of Hobq Desert (40°21′N, 109°51′E) in autumns of 2014 and 2015 (in Septemper and October). As a transitional zone of plateau desert and desert steppe, the region is a typical continental monsoon climate with an average elevation of 1040 m and an annual mean temperature is 6.1 °C (the lowest is −34.5 °C and the highest is 40.2 °C). The mean annual precipitation is 293 mm and the annual potential evapotranspiration is approximately 2400 mm. The soil texture is aeolian sandy soil, and large areas are shifting sand dunes with an average relative height of 5 m (Lan et al., 2010). Now there is a revegetation area of nearly 5000 m^2 formed by using inoculation-based" technology, and there are abundant biocrusts on sand surface. All are algae crusts (AC) or moss crusts (MC), but there is no lichen crust (LC) (Lan et al., 2010). Two ACs were dominated by *Microcoleus vaginatus* (AC1) and *Scytonema javanicum* (AC2), respectively. The dominant species in MC was *Byrum argenteum.* The two LCs in our experiments were sampled in the Shapotou Scientific Experimental Station at the southeast edge of Tengger Desert (37°32′N; 105°02′E), which was drier than Hobq Desert(Hu et al., 2002). LC1 was a kind of cyanolichen crusts dominated by *Collema* sp., and LC2 (dominated by *Placidium* sp.) was lichen crusts with green algae as photobiont.

Biocrusts were sampled with a 5 cm-diameter and 1cm-deep metal ring sampler and each type was divided into two groups (each group had at least 30 replications). Then one group was placed in sampler lids with the bottoms sealed whereas the other one was put in lids with gauze as bottom (water and gas can pass through freely). Coverage of the same biocrust type was kept basically the same. Biocrust samples were placed in open areas between sand dunes as soon as possible, more than 2 m away from vascular plants. The bottoms of biocrust samples were adjoined the sands below, and the upper surfaces of biocrusts were in the same horizontal plane with surrounding soil surface (Fig. A2)

2.2. Physicochemical characteristics

The physicochemical characteristics of the five types of biocrusts, which vary with the succession of biocrusts (Lan et al., 2015) and affect NRW accumulation, were determined in the lab just after sampling and shown in Table 1. Coverage of biocrusts was visually estimated on biocrust surface, as described by Wu et al. (2011). and thickness was measured with vernier calipers. Roughness was got by profile method (Römkens and Wang, 1986). Porosity and soil texture were measured by methods described by Lan et al. (2012). Salinity was measured with multiparameter water quality analyzer (YSI-Proplus, USA). The organic matter content and total biomass were determined based on the methods described by Lan et al. (2012, 2015). EPS was quantified according to the phenol-sulphuric acid method as described by Li et al. (2009). Chl-a content determination was conducted according to the description of Lan et al. (2011). In every measurement, each type of biocrusts had 3 duplications collected separately.

2.3. NRW measurements and the diurnal variation

The daily amount of NRW was determined using a scale (1/1000 precision), which was calculated from the weight difference of biocrusts between 18:00 h and 6:00 h in the next day (Lan et al., 2010) and converted to mm (Kidron et al., 2002). Besides, NRW of biocrusts was measured every 2 h from 18:00 h to 10:00 h in the next morning. According to the opinion of Agam and Berliner (2006), bottoms sealed experiments were also conducted. NRW in biocrusts with open bottoms had two water sources from atmosphere and soil, whereas NRW in samples with bottoms sealed was just from air. Measurements were conducted for 14 days in total. The measuring days were kept at least 3 days away from rainy days, and there is no heavy rain during the experimental period. The rainfall distribution during the experimental period was shown in Fig. A1. When measuring NRW, the outer surfaces of the lids containing crust samples were wiped with a dry cloth.

In NRW amount treatments, each biocrust type had 3 replications. In diurnal variation and source pattern measurements, each type had 5 replications. Shifting sand samples were set as control treatment. The key microclimate factors in experimental area were recorded by an automatic weather station (DZZ4, Jiangsu Radio Scientific Institute Co., LTD, China; integrated with WUSH-TW100 type high precision

Table 1
Characteristics of various biocrusts in different successional stages (mean ± s.e., n = 3).

	AC1	AC2	LC1	LC2	MC
Colour	Grey	Black brown	Black	Brown	Green
Surface morphology	Flat, without algal filament	Bit rough, with algal filament	Very rough, rosulate of thallus	Rough, crustose of thallus	Bit rough, blanket of moss
Dominant species	*Microcoleus vaginatus*	*Scytonema javanicum*	*Collema* sp.	*Placidium* sp.	*Byrum argenteum*
Coverage (%, dry/moist)	> 95/100	> 90/100	> 60/90	> 75/85	> 90/100
Location on dunes	Upper slope/evenly	Middle slope/evenly	Lower-middle part/mosaic patches	Lower slope/mosaic patches	Shady slope/inter- dunes/near shrubs
Roughness (mm)	1.34 ± 0.04[a]	1.72 ± 0.15[a]	3.36 ± 0.24[b]	5.02 ± 0.36[c]	4.56 ± 0.28[d]
Thickness (mm)	4.65 ± 0.52[a]	6.58 ± 0.54[b]	9.70 ± 0.86[c]	11.01 ± 0.78[d]	13.63 ± 0.74[e]
Sand content (%)	94.24 ± 0.18[a]	89.91 ± 0.39[b]	63.33 ± 1.35[c]	64.07 ± 0.23[c]	58.19 ± 0.07[d]
Silt and clay (%)	5.76 ± 0.16[a]	10.09 ± 0.45[b]	36.67 ± 1.34[c]	35.93 ± 0.18[c]	41.81 ± 0.08[d]
Porosity (%)	32.37 ± 0.13[a]	40.88 ± 1.48[b]	53.07 ± 1.61[c]	54.62 ± 0.75[c]	57.75 ± 0.47[d]
Salinity(PPT)	0.08 ± 0.01[a]	0.14 ± 0.01[b]	0.11 ± 0.01[c]	0.22 ± 0.01[d]	0.12 ± 0.00[e]
EPS (μg cm^{-2})	10.27 ± 0.08[a]	13.80 ± 1.84[a]	46.30 ± 3.47[b]	56.40 ± 1.52[c]	61.2 ± 2.03[d]
OM (mg cm^{-2})	6.63 ± 0.34[a]	12.92 ± 0.69[b]	41.42 ± 2.80[c]	46.75 ± 1.92[d]	80.52 ± 3.93[e]
Chl a (μg cm^{-2})	8.37 ± 0.57[a]	9.67 ± 0.98[a]	29.26 ± 2.05[b]	33.85 ± 3.81[bc]	37.60 ± 3.67[c]
Biomass (μmol CO_2 $h^{-1}cm^{-2}$)	1.41 ± 0.16[a]	1.88 ± 0.19[b]	2.75 ± 0.09[c]	3.30 ± 0.25[d]	4.91 ± 0.09[e]

The different superscript letters represent that the differences are significant ($P < 0.05$). EPS = Exopolysaccharides, OM = Organic matter, Chl *a* = Chlorophyll *a*.

temperature sensor), including temperature (air temperature, soil surface temperature, 5 cm soil temperature, dewpoint), air relative humidity, atmosphere pressure, and vapor pressure. Light radiation intensity was also measured synchronously with a light meter (Hansatech Instruments Ltd., UK).

2.4. Photosynthetic activities

Chlorophyll fluorescence of biocrusts was measured with a portable handheld PEA (Hansatech Instruments Ltd., UK) from 18:30 h to 9:00 h in the next morning and Fv/Fm values (indicating PS II activities) were recorded. Measurement interval was 2 h before 5:00 h and was 0.5 h after that. Light radiation intensity was measured synchronously with a light meter (Hansatech Instruments Ltd., UK). 8–10 replicates were set up for each biocrust type, and the PS II activities were monitored in 7 days.

2.5. CO_2 exchange

The carbon exchange rate of different biocrusts was determined by a soil carbon release rate determination device (Yaxinliyi Sci Technol Co., Ltd, China) brought to the field site. Measuring results were automatically calculated into μmol CO_2 $m^{-2}s^{-1}$ by the host system. Measurement interval was 1 h before 5:00 h, and 0.5 h after that. The CO_2 exchange was also monitored in 7 days. In this measurement, at least 30 replicates were set up for each biocrust type, and characteristics of the same type biocrusts were ensured to be as consistent as possible. At certain time point, CO_2 exchange five replications of each biocrust type were determined in the aforementioned measuring system. Then another five were measured, until all 30 replicates were detected and a new round of detection started. In this way, the disturbance of measuring operation on NRW accumulation was reduced to the minimum. Temperature and light intensity was recorded synchronously by automatic weather station (DZZ4, Jiangsu Radio Scientific Institute Co., LTD, China) and a light meter (Hansatech Instruments Ltd., UK).

2.6. Statistical analysis and modeling

The relationship between daily maximum NRW amount and physicochemical properties of biocrusts, and the main meteorological factors influencing the source proportions change of NRW were both analyzed by multiple regression analysis. The analysis was performed using SPSS 18.0 software. The influences of main nocturnal microclimate factors on NRW accumulation were analyzed using structural equation models through Amos 17.0 software.

3. Results

3.1. NRW accumulation and influencing factors

3.1.1. NRW accumulation pattern

NRW accumulation began from 18:00 h and reached a peak at 6:00 h, then decreased quickly after sunrise (Fig. 1a). Almost all NRW in shifting sand (SS) and biocrusts evaporated till 10:00 h except a small residual in MC. The real-time accumulation amount was significantly higher in biocrusts than in SS ($P < 0.05$) and followed in an ascending order of AC1, AC2, LC1, LC2, and MC. The pattern of daily maximum NRW amount (NRW_{max}) was also the same and the daily average NRW_{max} levels of SS, AC1, AC2, LC1, LC2 and MC were 0.038, 0.059, 0.093, 0.150, 0.180, and 0.219 mm, respectively.

3.1.2. NRW sources

Fig. 1b and c showed that higher proportions of NRW in MC and LC2 were from atmosphere (71% to 82%), whereas nearly half NRW in ACs was from soil (47% to 48%) and the other from atmosphere. The proportions in SS and LC1 remained relatively stable during 20:00–8:00 h, and no visible difference was observed between the two samples. Proportions of LC2 and MC were also stable during 20:00–4:00 h, later the atmosphere source percentage increased significantly during 4:00–6:00 h. No significant difference was also observed between the two biocrusts. Only the atmosphere source proportions in the two ACs continuously decreased and the proportion from soil persistently increased.

3.1.3. Factors influencing NRW sources

The influences of factors correlating to NRW sources (Table A1) were analyzed by regression analysis (Table 2). The source proportion of NRW in AC1 was mostly influenced by soil surface temperature, followed by vapor pressure that can partly reflect evaporation potential. The most significant factor influencing NRW sources in AC2 and LC1 was local atmospheric pressure, whereas for LC2 and MC it was temperature differential between soil surface and dewpoint. Overall, the effect of relevant temperatures was opposite to that of vapor pressure and atmosphere pressure.

3.1.4. Mechanism of NRW accumulation being influenced

During NRW accumulation in SS and AC1 (Fig. 2a and b), Ts

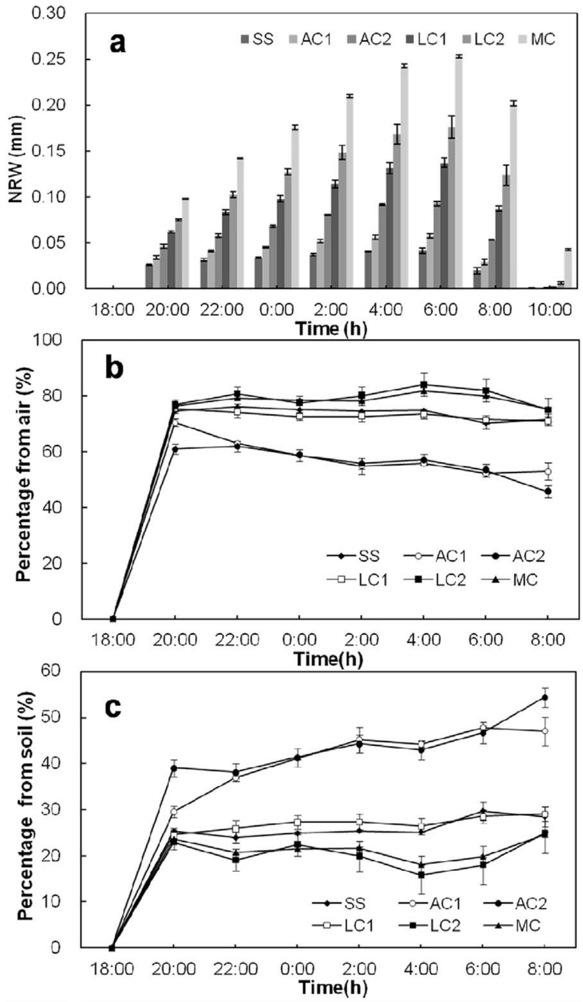

Fig. 1. (a) NRW accumulation patterns in SS and diverse biocrusts. (b) The proportions of NRW from atmosphere. (c) The proportions of NRW from soil. SS = Shifting sands. Data represents mean ± s.e. (data was from 14 days, each type of samples had 3 ~ 5 replications).

(surface temperature) and Ta (air temperature) were directly influenced by LI (light intensity). Then the changing Ts and Tb (temperature of 5 cm soil) which was directly influenced by it affected Ta, which further significantly affected RH (relative humidity). The two soil temperatures, especially Ts, together with RH had effects on NRW. The relationship between NRW accumulation and microclimate conditions was given in a structural equation model, which explained 57% and 66% variance of NRW accumulation in SS and AC1, respectively (Fig. 2a and b). The corresponding relationships for AC2 or LC1 were similar to that of SS and AC1 (R^2 = 0.71 in Fig. 2c and R^2 = 0.77 in Fig. 2d) except that NRW accumulation in AC2 and LC1 was directly influenced by LI. The degree of effect by soil temperature and RH also changed, but Ts still had the strongest influence on NRW (path coefficients were −0.52 and −0.38, respectively). For LC2 and MC (both R^2 = 0.78, Fig. 2e and f), the influence modes of microclimate conditions to NRW accumulation were similar to AC2 and LC1, but the degree of effect by LI and RH was higher than in other biocrusts. The influence of Tb was also higher than that of Ts.

For the relationship between biocrust attributes and daily NRW_{max} (Table 3), it showed that thickness had the strongest influence, followed by chl a content indicating photoautotroph biomass, and then EPS (exopolysaccharides), porosity, silt and clay, and organic matter. Although the influences of total biomass, roughness and salinity were also significant ($P < 0.01$), they were relatively weaker.

3.2. Photosynthetic activities recovery

With the NRW accumulation, the photosynthetic activities of AC began to recover stably from 20:30 h and decreased after sunrise, whereas LC2 and MC began to recover until 0:30 h and also decreased after sunrise (Fig. 3a). LC1 did not recover. The Fv/Fm value of AC was evidently higher than that of LC2 and MC during 19:30–0:30 h, whereas Fv/Fm of LC2 and MC had peak values during 3:30–6:30 h.

According to the ratio of Fv/Fm value to the characteristic value (the Fv/Fm value biocrusts can reach under ideal conditions), LC1 was proven to not show recovery (Fig. 3b). ACs recovered earliest, and the recovery degree was higher than in LC2 and MC during 18:30–0:30 h, finally reaching 44% to 50% of the characteristic value until 5:30–6:30 h. LC2 and MC recovered later but had the highest recovery degree during 3:30–6:30 h (75%–84%).

To further clarify the recovery degree of photosynthetic activities, the ratio of Fv/Fm value at different time points to the highest value that night was analyzed (Fig. 3c). The ratio of LC1 fluctuated slightly. But up to 20:30 h, the Fv/Fm of AC had achieved more than 50% of the maximum value of that night and then reached over 70% during 23:30–7:30 h. The ratio of LC2 and MC reached over 50% after 2:30, then over 70% during 3:30 –7:30 h.

The main microclimate parameters during NRW duration (Fig. 3d) showed that surface temperature declined rapidly, whereas air temperature rapidly decreased at first and then slowed down. The dew point temperature decreased slightly. Air relative humidity continued to increase slowly after a short abrupt increase. Sunrise was at about 6:30 h, light intensity was usually 3–15 μmol m^{-2} s^{-1} between 5:30 and 6:30 h but 2–3 μmol m^{-2} s^{-1} during 21:00 h −5:30 h (Fig. 3e).

Table 2
The multiple regression analysis of relationships between source proportion variation of NRW in biocrusts and nocturnal meteorological factors.

		Unstandardized Coefficients		Standardized Coefficients	t	Sig
		B	Std. Error	Beta		
AC1	Constant	49.991	5.149		9.708	0.001
	Ts	−2.417	0.213	−1.070	−11.323	0.000
	VP	2.176	0.676	0.304	3.217	0.032
AC2	Constant	−9489.277	2145.719		−4.422	0.007
	AP	10.529	2.370	0.893	4.443	0.007
LC1	Constant	−2892.878	341.916		−8.461	0.000
	AP	3.225	0.378	0.967	8.540	0.000
LC2	Constant	29.468	2.734		10.780	0.000
	TD-ad	−3.502	1.026	−0.837	−3.414	0.019
MC	Constant	27.849	1.851		15.044	0.000
	TD-ad	−2.488	0.695	−0.848	−3.582	0.016

VP = Vapor pressure, AP = Atmospheric pressure, TD-ad = Temperature difference between air and dew point.

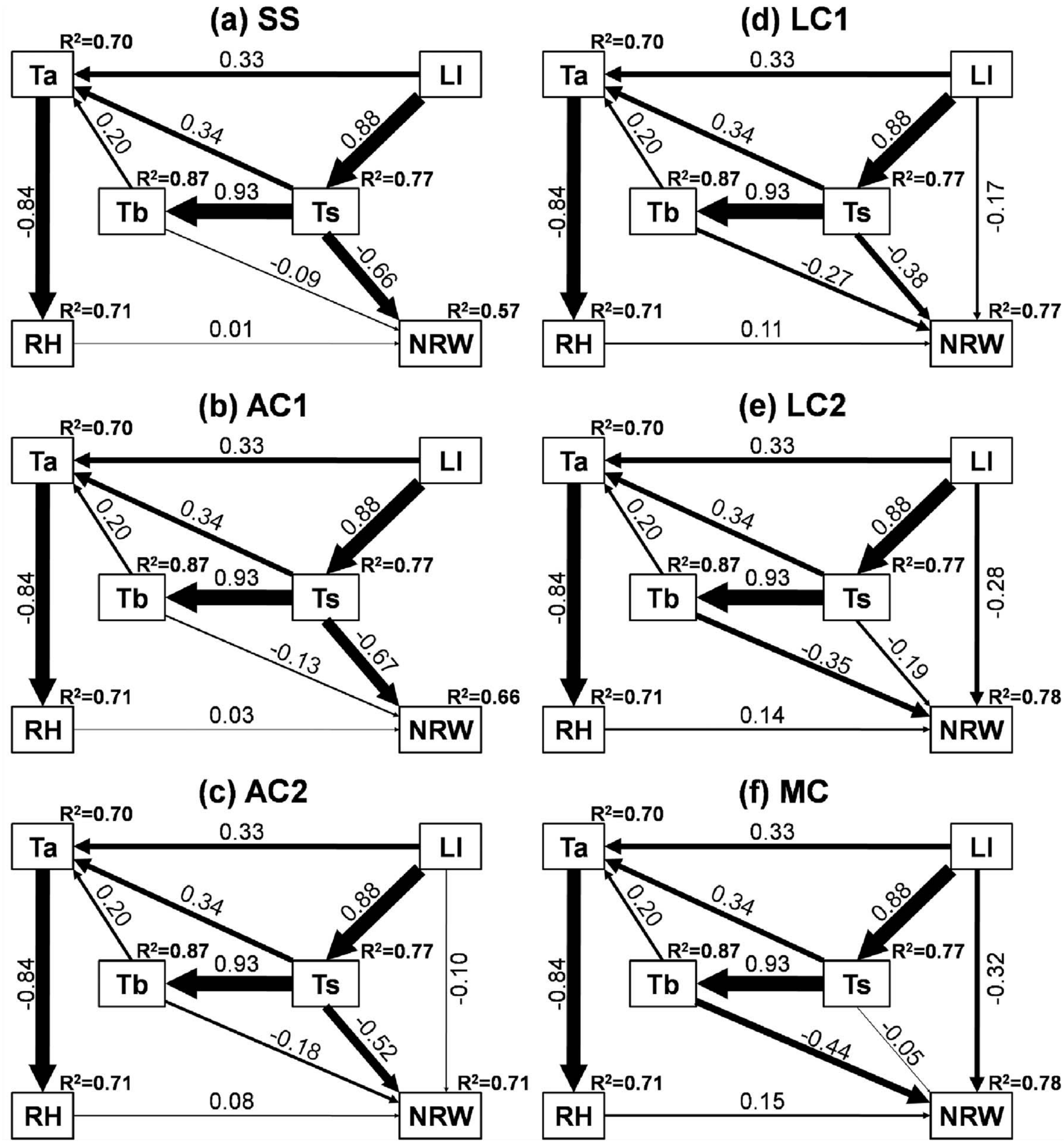

Fig. 2. The effects of main meteorological factors on NRW ammount during the night. The width of each arrow is proportionate to the path coefficient. SS = Shifting sands. LI = Light intensity, Ta = Temperature of air, Tb = Temperature of soil 5 cm below the surface, Ts = Temperature of soil surface, RH = Relative humidity.

Table 3
The influence of biocrusts physicochemical characteristics on daily maximum NRW analyzed by multiple regression analysis.

	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
Constant	−0.066	0.009		−7.152	0.000
Thickness	0.022	0.001	0.988	22.958	0.000
Chl a	0.001	0.000	0.956	11.720	0.000
EPS	0.003	0.000	0.954	11.408	0.000
Porosity	0.007	0.001	0.941	10.040	0.000
Silt and clay	0.004	0.001	0.921	8.512	0.000
Organic matter	0.002	0.000	0.920	−0.101	0.000
Total biomass	0.038	0.005	0.663	8.417	0.000
Roughness	0.017	0.004	0.362	4.598	0.001
Salinity	0.313	0.062	0.200	5.046	0.000

EPS = Exopolysaccharides, Chl a = Chlorophyll *a*.

3.3. CO_2 exchange

When NRW in one day approached the local average daily NRW in September, consumptive carbon exchange was observed from 0:30 h (Fig. 4a). AC1 firstly obtained net carbon uptake at 6:00 h, followed by AC2, LC2, and MC at 6:30 h (sunrise), and peak values were in the order of MC > LC2 > AC. After carbon input lasted for 2–3 h, carbon loss reappeared briefly. However, no carbon input was detected in LC1. When NRW was far below the daily average value, there was no net carbon input in any biocrusts (Fig. 4d). Carbon loss began from 1:30 h, and diurnal carbon deficit was in the following order: MC > LC2 > LC1 ≈ AC2 > AC1. When NRW exceeded the daily average, carbon consumption started from 23:30 h (Fig. 4g). The duration of net carbon uptake was also extended to about 9:20 h because the weather turned cloudy in the morning, resulting in a higher diurnal net carbon income.

Based on experimental data in September of 2014 to 2015, the relationships between daily NRW_{max} and net carbon balance of biocrusts

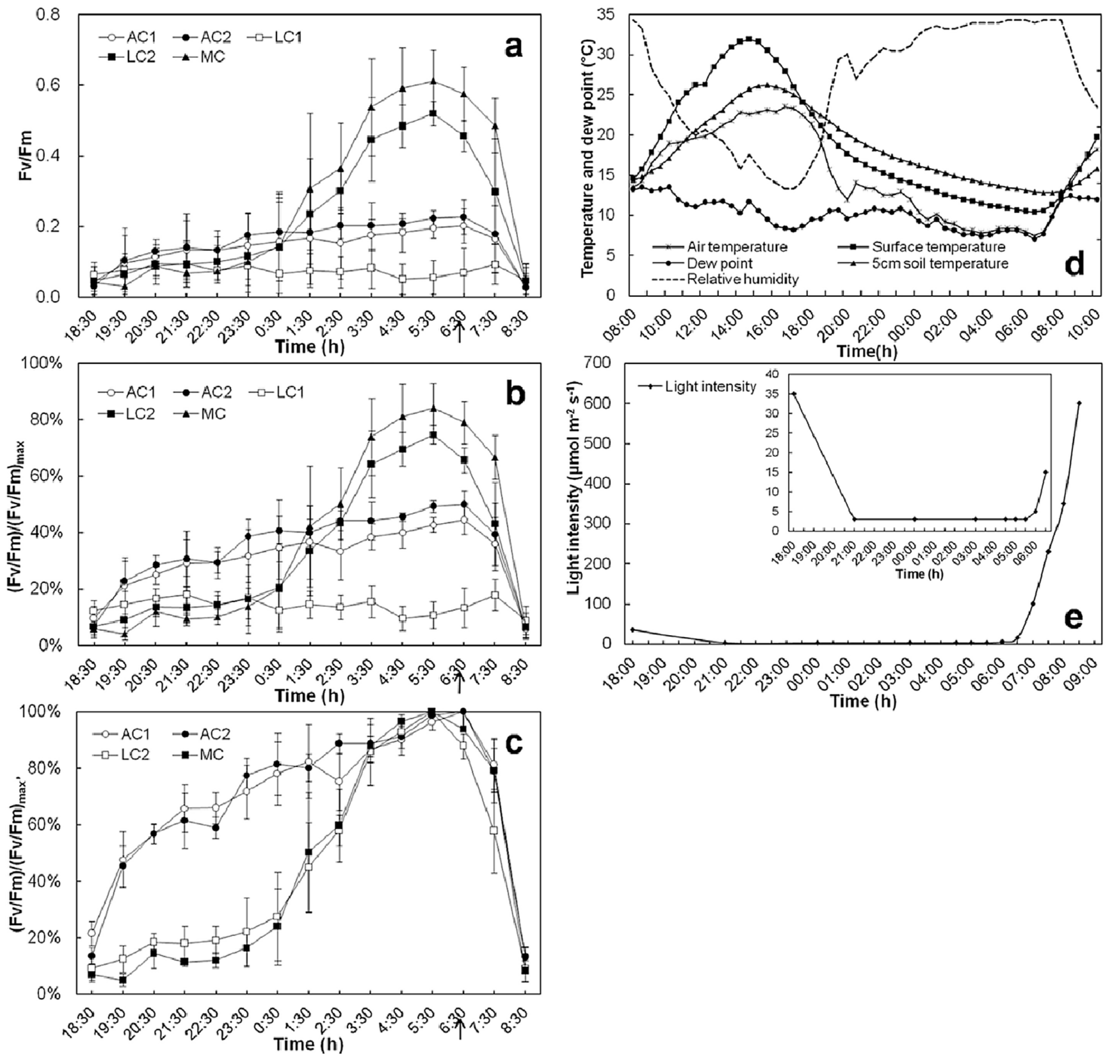

Fig. 3. The recovery of photosynthetic activities of biocrusts during accumulation of NRW, which was measured at 1 h interval during 13–14 September 2015. (a) Fv/Fm values of biocrusts; (b) the ratio of Fv/Fm value to its characteristic value (that is, the Fv/Fm value BSCs can reach under ideal conditions); (c) the ratio of Fv/Fm value to the maximum Fv/Fm value in that night. Arrows indicate sunrise. Data represents mean ± s.e. (n = 8 ~ 10). (d) Daily variations of microclimate conditions observed at 0.5 h interval. (e) The light intensity during NRW accumulation. The internal panel showed the variation of light before sunrise.

were analyzed, and regression equations were obtained (Table 4). A more direct relationship between daily NRW_{max} and carbon balance was found in MC. The relationship in LC2 was more complicated but was similar in AC1 and AC2. According to the relationships and the net carbon balance of various biocrusts, the minimum diel NRW required by ACs, LC2, and MC to maintain carbon balance were estimated, which were about 0.08, 0.17, and 0.20 mm, respectively. And based on the actual carbon balance observed in the field, the carbon input duration was considered to be more than 2 h.

4. Discussion

Based on the principle that NRW formation was influenced by climate, weather, and soil surface traits (Wang et al., 2014; Kidron et al., 2000; Kidron and Termina, 2013), our results showed that LI was the driving force of biocrust promotion of NRW accumulation. It does not only directly influence on Ts and Ta but also indirectly on Tb and RH. It is especially notable that biocrust characteristics had feedback on the degree of effect by LI, Ts, Tb, and RH on NRW accumulation, and the feedback strength was linearly correlated with the development level of biocrusts. Specially, the direct effect of LI and indirect effects of Tb and air RH enhanced gradually with the succession of biocrusts, whereas the influence of Ts decreased. We thought the greater impact of LI on NRW of dark biocrusts (AC2 and LC1) was mainly because dark pigments on surface reflected less optical radiation (Kidron and Tal, 2012), whereas the greater influence on NRW of light biocrusts in later succession stages was mainly related to the increase of photoautotroph biomass. NRW in ACs and LC1 was influenced greater by Ts because of the poor regulating ability of lower thickness than LC2 and MC (Table 1), which was further weakened by the warming resulting from dark pigments (Couradeau et al., 2016). NRW in LC2 and MC being mainly affected by Tb was also attributed to the regulating effect of thickness because temperature difference could be detected only when thickness achieved a specific value (Liu et al., 2006). The influence of RH augmenting with development of biocrusts may be due to the increase of roughness (Ahmadjian, 1993; Kidron et al., 2002; Tao and Zhang, 2012), which not only included the surface undulation of biocrust morphology but also morphological structure complexity and ecological niches of cryptogams. For instance, dominant species *Microcoleus vaginatus* in AC1 was mostly in depth of below 20 μm, whereas dominant species *Scytonema javanicum* in AC2 was mainly on the topmost surface (Hu et al., 2003a).

NRW accumulation in biocrusts started from sunset and reached the peak value at sunrise, after which it decreased rapidly. The pattern was similar to the result of Zhang et al. (2009), and no double peak phenomenon was observed (Liu et al., 2006; Rao et al., 2009). This

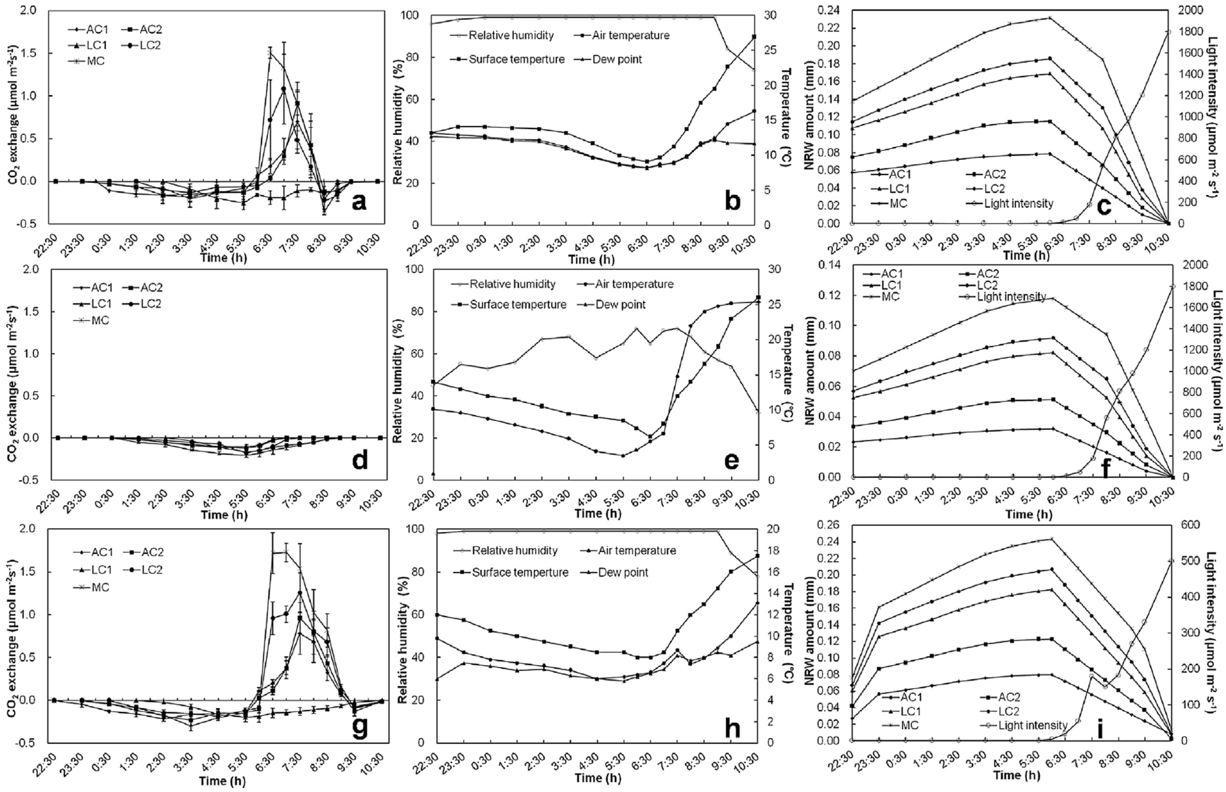

Fig. 4. Three typical CO_2 exchange patterns of biocrusts during NRW accumulation. Synchronous microclimate parameters and NRW amount were also determined. (a) Each type of biocrusts had net carbon input. (d) Carbon loss emerged in all biocrusts when NRW was much less than daily average. (g) Biocrusts had greater net carbon input. (b), (e), (h) display the synchronous microclimate parameters of (a), (d), (g); (c), (f) and (i) show the light intensity and NRW amount dynamics during the CO_2 exchange of biocrusts.

Table 4
Relationship model of carbon balance and daily maximum NRW in different biocrusts.

	Regression equation	R^2
AC1	$Y = -154.481X^3 + 2.092X - 0.078$	0.893
AC2	$Y = -55.257X^3 + 1.883X - 0.107$	0.960
LC2	$Y = -3.759X^3 + 3.733X^2 - 0.054$	0.994
MC	$Y = 0.901X^2 + 0.827X - 0.148$	0.993

X = daily maximum NRW, Y = carbon balance.

observation may be related to air pressure change during the measurements.

Nocturnal NRW_{max} in biocrusts was supposed to be associated with roughness, EPS, soil texture, and salinity (Kosmas et al., 2001; Kidron et al., 2002; Zhang et al., 2009; Lan et al., 2010; Chen et al., 2014; Wang et al., 2014). Our results showed that it also correlated significantly with many other attributes of biocrusts, among which thickness had the strongest effect, followed by biomass of photosynthetic organisms, then EPS, porosity, silt and clay, and organic matter (Hu et al., 2003b; Lan et al., 2010; Fischer et al., 2012; Chen et al., 2014; Colica et al., 2014). The influence of total biomass, roughness, and salinity was relatively smaller. The diel NRW_{max} was different from water absorbing capacity or water retaining capacity because the effects of roughness (Ahmadjian, 1993; Kidron et al., 2002; Tao and Zhang et al., 2012), salinity (Li et al., 2013), and organism remains (Delgado-Baquerizo et al., 2013) were not so remarkable as originally thought. On the contrary, photoautotroph biomass in biocrusts made great contributions to NRW. The effects of EPS and organic matter (del Prado and Sancho, 2007; Lan et al., 2011, 2015) were presumed to also mainly stem from photoautotrophs. Therefore, under the carrying capacity determined by thickness, the biomass of cryptogams and its related attributes played an important role in regulating diel NRW_{max}.

NRW in biocrusts had two sources that came from atmosphere and soil, respectively, but it was proven that 60% to 75% of NRW was from the soil in artificial biocrusts (Lan et al., 2010). Although the proportion of NRW from soil in natural ACs was lower than that of artificial AC, it was still much higher than in LC and MC. Based on the theory that soil water vapor movement was driven by humidity and temperature gradient, we suggested that meteorological parameters significantly related to NRW sources (vapor pressure, atmospheric pressure, surface temperature, and temperature difference between air and dew point) could reflect the drive strength. The higher proportion of NRW from soil in AC was due to the strong capillary effect driven by vapor pressure and atmospheric pressure (Agama and Berliner, 2006; Lan et al., 2010). It also can be considered to be the result of low roughness that led to less moisture from the atmosphere and distinct humidity gradient from below to top. NRW in LC2 and MC had a high proportion of source from the atmosphere, because temperature differential between surface and dew point made them, which had high roughness, obtain more moisture from atmosphere, and such a humidity gradient was unfavorable for the upward movement of soil capillary water. NRW in biocrusts dominated by green-algae lichens was mainly contributed by water vapor absorption (Uclés et al., 2015).

NRW in AC1 and AC2 had similar source pattern, so did LC2 and MC, which was easy to understand because they had similar properties. However, it was peculiar that the source patterns of LC1 and SS from atmosphere and soil were very alike at almost all different time points, regardless of the absolute NRW amount in LC1 being much higher than that in SS. We supposed that it was definitely not a simple coincidence but resulted from the comprehensive function of various properties of the two surface types. Photosynthetic activities of LC1 did not recover during NRW accumulation, which was most similar to SS. The attributes of LC1 and LC2 were similar. Therefore, the source patterns of NRW in biocrusts may be regulated by the degree of photosynthetic activities, such as actively absorbing water, growth, and metabolism. The nocturnal variation of different source proportions of NRW in LC and MC was comparatively stable, whereas the proportion from atmosphere in AC kept decreasing slowly. We assumed that greater temperature gradient, atmospheric pressure, and vapor pressure enhanced the capillary effect in AC, whereas porosity and humidity gradient in LC and MC were not conducive to capillary action.

Potential value of Fv/Fm in biocrusts was a characteristic value of the dominant cryptogams' genetic evolution, but the recovery level and recovery rate could reflect the adaptability of dominant cryptogams. Lange (2003) showed that the photosynthetic activities could be activated by NRW in heavy fog coastal desert, and effective carbon sequestration emerged. However, only photosynthetic activity of lichen biocrusts was in situ detected (Veste et al., 2001). In our study, although field Fv/Fm recovery values of biocrusts were inferior to their theoretical value, all biocrusts except for LC1 initiated photosynthetic activities and lasted to the next morning when NRW was 0.05 mm or so. The time to start recovery of AC was earlier than that of LC2 and MC. From 19:30 h on, recovery degree of AC had approached 50% of the maximum recovery value in that night, although real-time recovery value was just 21% of the theoretical value. Nocturnal low temperature and poor light had no effect on photosynthetic activity initiation. AC utilized NRW in a way of longer time and lower efficiency, whereas LC2 and MC in a way of shorter time and higher efficiency.

The CO_2 exchange patterns of biocrusts were similar to lichen thallus in heavy fog coastal desert and saxicolous lichens in temperate zone (Lange et al., 1997; Lange, 2003), moss in semi-arid grasslands (Csintalan et al., 2000), and arboreal lichens (Lange et al., 2001), so was the exchange magnitude, except for lichen thallus in heavy fog coastal desert having a higher one. According to simulation equations, daily maximum NRW amount had the most remarkable effect on carbon balance of MC. The relationship was more complicated in LC2, which may result from that LC2 could also be affect by water vapor other than liquid water. The relationship complexity in ACs were between the former two, indicating that the influence of NRWmax on carbon balance in ACs was not so direct and effective as that in MC, but was still more effective than that in LC2. When diel NRW approached the local average in September, the final net carbon gains of AC1, AC2, LC2, and MC were 0.0061, 0.015, 0.0361, and 0.0619 g C m^{-2}, respectively, after carbon consumption was deducted. When the morning weather turned into cloudy before the evaporation of NRW, the net carbon gains of AC1, AC2, LC2, and MC were 0.012, 0.025, 0.073, and 0.107 g C m^{-2}, respectively. The required diel NRW_{max} for biocrusts to maintain carbon balance was 0.08 mm for AC1, 0.09 mm for AC2, ca. 0.17 mm for LC2, and ca. 0.20 mm for MC. Therefore, AC1 may have more chances to survive and develop than other biocrusts in water-limited areas because of its minimum water requirements. It is why inoculation-based technology can more easily be achieved when starting with AC1.

Although biocrusts distribute globally in arid, semi-arid and dry subhumid regions, microhabitats are more effective for biocrust biomass (Lan et al., 2011; Fischer and Subbotina, 2014). For carbon fixation of biocrusts using dew, Lange et al. (1992) found photosynthetic activities of biocrusts were inhibited at liquid water content less than 0.1 mm. Kidron et al. (2002) and Veste and Littmann (2006) further determined 0.1 mm dewfall was necessary for net photosynthesis of AC and chlorolichen crusts. But we have found the recovery level of PS II change with water content (Wu et al., 2013a), AC1 could activate at 0.05 mm or so in situ (Fv/Fm only ca. 21% of ideal Fv/Fm). So although the 0.08–0.09 mm threshold seemed close to their 0.1 mm, the essence was quite different, because this threshold derived from carbon balance under real-time NRW, considering the duration, time-point and carbon loss. Of course, NRW is often a supply for precipitation in drylands, microclimate conditions maintaining biocrusts must also obey zone characteristics, so the drier zone, the higher the threshold required by biocrusts to obtain positive carbon balance might be. But even in hyperarid environment, the special microhabitats with moist subsoil and abundant nucleation on the topsoil might not be as high as our zone. Nevertheless, the 0.08 mm threshold has been confirmed by *Microcoleus vaginatus* dominated biocrusts in Mu Us and Horqin sand land, Hobq, Ulan Buh and Hulun Buir desert (Zheng et al., 2011; Hu et al., 2012; Lan et al., 2014). It is the lowest value in inland aeolian sandy soil of China (250–400 mm annual precipitation). We guessed it might also be global lowest value in similar environments. But it must be pointed out, the threshold is a proposed value base on *Microcoleus vaginatus* dominated biocrusts and different from that of shifting sand, so it needs to be more evaluated when consider and use.

5. Conclusions

Light intensity, surface temperature, 5 cm subsoil temperature, and air relative humidity were significant meteorological factors that influenced NRW accumulation in biocrusts. But biocrust attributes also had remarkable feedback regulation on NRW accumulation, and the feedback intensity had a linear correlation with development level of

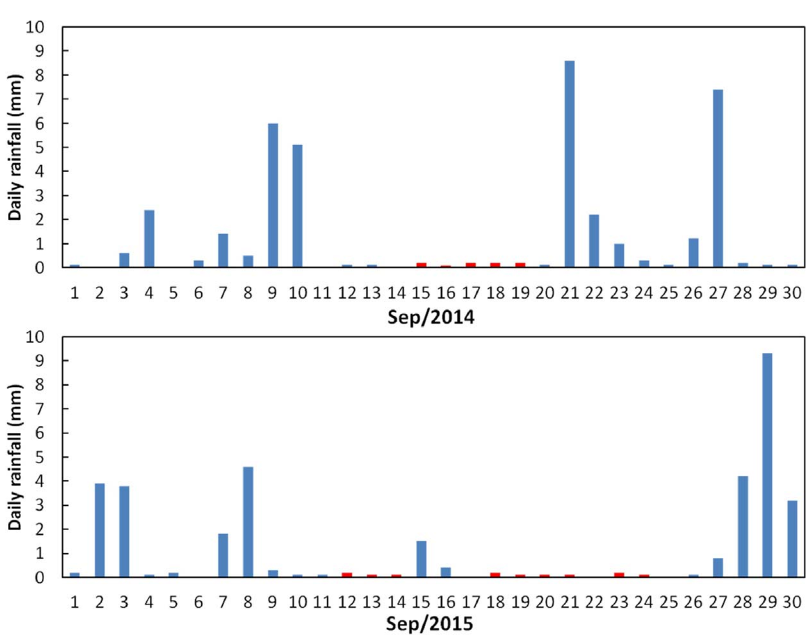

Fig. A1. Rainfall distribution during the experimental period. The dates in which NRW was measured were highlighted in red.

Fig. A2. Photograph of the sampler lids with biocrusts in the field.

Table A1
Correlation analysis between variation of NRW proportion from soil and meteorological factors (the proportion from atmosphere is exactly opposite and not listed here).

	Ta	RH	VP	AP	Ts	Tb	TD-ad	TD-as	TD-sb
SS	−0.390	0.229	−0.498	0.667	−0.703	−0.754	−0.229	−0.134	0.103
AC1	−0.745	0.747	−0.134	0.917**	−0.945**	−0.942**	−0.778*	0.203	0.385
AC2	−0.237	0.208	−0.070	0.893**	−0.708	−0.853**	−0.241	−0.407	−0.214
LC1	−0.484	0.517	0.048	0.967**	−0.812*	−0.881**	−0.557	−0.096	0.084
LC2	0.694	−0.549	0.616	0.092	0.378	0.177	0.527	−0.773*	−0.837*
MC	0.725	−0.640	0.449	0.037	0.387	0.184	0.623	−0.816*	−0.848*

SS = Shifting sands. Ta = Temperature of air, RH = Relative humidity, VP = Vapor pressure, AP = Atmospheric pressure, Ts = Temperature of crustal surface, Tb = Temperature of 5 cm below the surface, TD-ad = Temperature difference between air and dew point, TD-as = Temperature difference between air and surface, TD-sb = Temperature difference between surface and soil 5 cm below.

* Represents significant ($P < 0.05$).

** Tepresents very significant ($P < 0.01$).

biocrusts, fully embodying the consistency between development and succession degree of biocrusts and their feedback function.

Although local air pressure, vapor pressure, surface temperature, and temperature difference of air and dew point in the night were important meteorological factors that affected different source proportions of NRW, the specific percentages of the two sources were also regulated by activities of photoautotrophs in biocrusts. Under the carrying capacity determined by thickness, the biomass of cryptogams and its related attributes also contributed to the regulation of the daily NRWmax.

NRW was not only the most frequent water source in arid and semiarid areas, but also the most frequent water for the photosynthetic carbon fixation of cryptogams in biocrusts (LC1 excluded). During NRW accumulation, photosysetem II activities of cryptogams remained for a long time under low temperature and poor light and had made physiological preparations to utilize NRW for carbon fixation. Biocrusts in early succession stages (ACs) fixed carbon by a strategy of lower efficiency and longer time, whereas those in later succession stages (LC2 and MC) by a strategy of higher efficiency and shorter time.

According to the daily carbon balance of different types of biocrusts utilizing NRW, we suggested the land boundary of inoculation-based technology in drylands might be in the areas where daily NRW_{max} exceed or equal 0.08 mm during NRW-abundant seasons. Meanwhile, carbon input under NRW in the morning should last more than 2 h.

Acknowledgments

This work was financially supported by the National Natural Science Foundation of China (41573111, 31670456, 31300322). Thanks for Qiaoning He to provide assistance in the field work.

Appendix A

References

Agam, N., Berliner, P.R., 2006. Dew formation and water vapor adsorption in semi-arid environments-a review. J. Arid Environ. 65 (4), 572–590.

Ahmadjian, V., 1993. The lichen photobiont: what can it tell us about lichen systematics? Bryologist 96 (3), 310–313.

Belnap, J., Lange, O.L., 2001. Structure and functioning of biological soil crusts: a synthesis. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Springer, Berlin Heidelberg, pp. 471–479.

Bowker, M.A., 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restor. Ecol. 15 (1), 13–23.

Chen, L., Rossi, F., Deng, S., Liu, Y.D., Wang, G.H., Alessandra, A., De Philippis, R., 2014. Macromolecular and chemical features of the excreted extracellular polysaccharides in induced biological soil crusts of different ages. Soil Biol. Biochem. 78, 1–9.

Chiquoine, L.P., Abella, S.R., Bowker, M.A., 2016. Rapidly restoring biological soil crusts

and ecosystem functions in a severely disturbed desert ecosystem. Ecol. Appl. 26 (4), 1260–1272.
Coe, K.K., Belnap, J., Sparks, J.P., 2012. Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. Ecology 93, 1626–1636.
Colica, G., Li, H., Rossi, F., Li, D.H., Liu, Y.D., De Philippis, R., 2014. Microbial secreted exopolysaccharides affect the hydrological behavior of induced biological soil crusts in desert sandy soils. Soil Biol. Biochem. 68, 62–70.
Couradeau, E., Karaoz, U., Lim, H.C., da Rocha, U.N., Northen, T., Brodie, E., Garcia-Pichel, F., 2016. Bacteria increase arid-land soil surface temperature through the production of sunscreens. Nat. Commun. 7.
Csintalan, Z., Takács, Z., Proctor, M.C.F., Nagy, Z., Tuba, Z., 2000. Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland. Plant Ecol. 151 (1), 51–54.
Darrouzet-Nardi, A., Reed, S.C., Grote, E.E., Belnap, J., 2015. Observations of net soil exchange of CO_2 in a dryland show experimental warming increases carbon losses in biocrust soils. Biogeochemistry 126 (3), 363–378.
del Prado, R., Sancho, L.G., 2007. Dew as a key factor for the distribution pattern of the lichen species *Teloschistes lacunosus* in the Tabernas Desert (Spain). Flora 202 (5), 417–428.
Delgado-Baquerizo, M., Maestre, F.T., Rodríguez, J.G.P., Gallardo, A., 2013. Biological soil crusts promote N accumulation in response to dew events in dryland soils. Soil Biol. Biochem. 62, 22–27.
Evenari, M., Shanan, L., Tadmor, N., 1971. The Negev. The Challenge of a Desert.
Feng, W., Zhang, Y.Q., Wu, B., Qin, S.G., Lai, Z.R., 2014. Influence of environmental factors on carbon dioxide exchange in biological soil crusts in desert areas. Arid Land Res. Manag. 28 (2), 186–196.
Fischer, T., Subbotina, M., 2014. Climatic and soil texture threshold values for cryptogamic cover development: a meta analysis. Biologia 69 (11), 1520–1530.
Fischer, T., Veste, M., Bens, O., Hüttl, R.F., 2012. Dew formation on the surface of biological soil crusts in central European sand ecosystems. Biogeosciences 9 (11), 4621–4628.
Heusinkveld, B.G., Berkowicz, S.M., Jacobs, A.F.G., Holtslag, A.A.M., Hillen, W.C.A.M., 2006. An automated microlysimeter to study dew formation and evaporation in arid and semiarid regions. J. Hydrometeorol. 7 (4), 825–832.
Housman, D.C., Powers, H.H., Collins, A.D., Belnap, J., 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. J. Arid Environ. 66 (4), 620–634.
Hu, C.X., Liu, Y.D., Zhang, D.L., Huang, Z.B., Paulsen, B.S., 2002. Cementing mechanism of algal crusts from desert area. Chin. Sci. Bull. 47 (16), 1361–1368.
Hu, C.X., Liu, Y.D., Paulsen, B.S., Petersen, D., Klaveness, D., 2003a. Extracellular carbohydrate polymers from five desert soil algae with different cohesion in the stabilization of fine sand grain. Carbohyd. Polym. 54 (1), 33–42.
Hu, C.X., Zhang, D.L., Huang, Z.B., Liu, Y.D., 2003b. The vertical microdistribution of cyanobacteria and green algae within desert crusts and the development of the algal crusts. Plant Soil 257 (1), 97–111.
Hu, C.X., Gao, K.S., Whitton, B.A., 2012. Semi-arid regions and deserts. In: Whitton, B.A. (Ed.), Ecology of Cyanobacteria II: Their Diversity in Space and Time. Springer Science + Business Media, Dordrecht, pp. 345–369.
Huang, L., Zhang, Z.S., Li, X.R., 2014. Carbon fixation and its influence factors of biological soil crusts in a revegetated area of the Tengger Desert, northern China. J. Arid Land 6 (6), 725–734.
Jeffries, D.L., Link, S.O., Klopatek, J.M., 1993. CO_2 fluxes of cryptogamic crusts. New Phytol. 125 (1), 163–173.
Kaseke, K.F., Mills, A.J., Esler, K., Henschel, M.K., Brown, R., 2012. Spatial variation of non-rainfall water input and the effect of mechanical soil crusts on input and evaporation. Pure Appl. Geophys. 169 (12), 2217–2229.
Kidron, G.J., Tal, S.Y., 2012. The effect of biocrusts on evaporation from sand dunes in the Negev Desert. Geoderma 179, 104–112.
Kidron, G.J., Temina, M., 2013. The effect of dew and fog on lithic lichens along an altitudinal gradient in the Negev Desert. Geomicrobiol. J. 30 (4), 281–290.
Kidron, G.J., Yair, A., Danin, A., 2000. Dew variability within a small arid drainage basin in the Negev Highlands, Israel. Q. J. Roy. Meteorol. Soc. 126 (562), 63–80.
Kidron, G.J., Herrnstadt, I., Barzilay, E., 2002. The role of dew as a moisture source for sand microbiotic crusts in the Negev Desert, Israel. J. Arid Environ. 52 (4), 517–533.
Kidron, G.J., 2000. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmos. Res. 55 (3), 257–270.
Kosmas, C., Marathianou, M., Gerontidis, S., Detsis, V., Tsara, M., Poesen, J., 2001. Parameters affecting water vapor adsorption by the soil under semi-arid climatic conditions. Agric. Water Manag. 48 (1), 61–78.
Lan, S.B., Hu, C.X., Rao, B.Q., Wu, L., Zhang, D.L., Liu, Y.D., 2010. Non-rainfall water sources in the topsoil and their changes during formation of man-made algal crusts at the eastern edge of Qubqi Desert, Inner Mongolia. Sci. China Life Sci. 53 (9), 1135–1141.
Lan, S.B., Wu, L., Zhang, D.L., Liu, Y.D., 2011. Ethanol outperforms multiple solvents in the extraction of chlorophyll-a from biological soil crusts. Soil Biol. Biochem. 43 (4), 857–861.
Lan, S.B., Wu, L., Zhang, D.L., Hu, C.X., 2012. Successional stages of biological soil crusts and their microstructure variability in Shapotou region (China). Environ. Earth Sci. 65 (1), 77–88.
Lan, S.B., Wu, L., Zhang, D.L., Hu, C.X., 2014. Desiccation provides photosynthetic protection for crust cyanobacteria *Microcoleus vaginatus* from high temperature. Physiol. Plant. 152 (2), 345–354.
Lan, S.B., Wu, L., Zhang, D.L., Hu, C.X., 2015. Analysis of environmental factors determining development and succession in biological soil crusts. Sci. Total Environ. 538, 492–499.
Lange, O.L., Kidron, G.J., Budel, B., Meyer, A., Lilian, E., Abeliovich, A., 1992. Taxonomic composition and photosynthetic characteristics of thebiological soil crusts' covering sand dunes in the western Negev Desert. Funct. Ecol. 519–527.
Lange, O.L., Reichenberger, H., Walz, H., 1997. Continuous monitoring of CO_2 exchange of lichens in the field: short-term enclosure with an automatically operating cuvette. Lichenologist 29 (3), 259–274.
Lange, O.L., Green, T.G.A., Heber, U., 2001. Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance? J. Exp. Bot. 52 (363), 2033–2042.
Lange, O.L., 2003. Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: long-term field monitoring of CO_2 exchange and its physiological interpretation: II. Diel and seasonal patterns of net photosynthesis and respiration. Flora 198 (1), 55–70.
Li, D.H., Xing, W., Li, G.B., Liu, Y.D., 2009. Cytochemical changes in the developmental process of *Nostoc sphaeroides* (cyanobacterium). J. Appl. Phycol. 21, 119–125.
Li, X.R., Zhang, P., Su, Y.G., Jia, R.L., 2012. Carbon fixation by biological soil crusts following revegetation of sand dunes in arid desert regions of China: a four-year field study. Catena 97, 119–126.
Li, X.R., Zhang, Z.S., Huang, L., Wang, X.P., 2013. Review of the ecohydrological processes and feedback mechanisms controlling sand-binding vegetation systems in sandy desert regions of China. Chin. Sci. Bull. 58 (13), 1483–1496.
Liu, L.C., Li, S.Z., Duan, Z.H., Wang, T., Zhang, Z.S., Li, X.R., 2006. Effects of microbiotic crusts on dew deposition in the restored vegetation area at Shapotou, northwest China. J. Hydrol. 328 (1), 331–337.
Liu, Y.D., Hu, C.X., Zhang, W.J., 2013. Environmental Biology of Desert Cyanobacteria and Combating Desertification with Biological Soil Crust. Science Press, Beijing.
Malek, E., McCurdy, G., Giles, B., 1999. Dew contribution to the annual water balances in semi-arid desert valleys. J. Arid Environ. 42 (2), 71–80.
Mallen-Cooper, M., Eldridge, D.J., 2016. Laboratory-based techniques for assessing the functional traits of biocrusts. Plant Soil 406, 131–143.
Pan, Y.X., Wang, X.P., Zhang, Y.F., 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area, Northern China. J. Hydrol. 387 (3), 265–272.
Römkens, M.J., Wang, J.Y., 1986. Effect of tillage on surface roughness. Trans. ASAE 29 (2), 429–433.
Rao, B.Q., Liu, Y.D., Wang, W.B., Hu, C.X., Li, D.H., Lan, S.B., 2009. Influence of dew on biomass and photosystem II activity of cyanobacterial crusts in the Hopq Desert, northwest China. Soil Biol. Biochem. 41 (12), 2387–2393.
Reed, S.C., Coe, K.K., Sparks, J.P., Housman, D.C., Zelikova, T.J., Belnap, J., 2012. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. Nat. Clim. Change 2, 752–755.
Rossi, F., Li, H., Liu, Y., De Philippis, R., 2017. Cyanobacterial inoculation (cyanobacterisation): perspectives for the development of a standardized multifunctional technology for soil fertilization and desertification reversal. Earth-Sci. Rev. 171, 28–43.
Su, Y.G., Li, X.R., Qi, P.C., Chen, Y.W., 2012. Carbon exchange responses of cyanobacterial-algal crusts to dehydration, air temperature, and CO_2 concentration. Arid Land Res. Manag. 26 (1), 44–58.
Su, Y.G., Wu, L., Zhou, Z.B., Zhang, Y.M., 2013. Carbon flux in deserts depends on soil cover type A case study in the Gurbantunggute desert, North China. Soil Biol. Biochem. 58, 332–340.
Tao, Y., Zhang, Y.M., 2012. Effects of leaf hair points of a desert moss on water retention and dew formation: implications for desiccation tolerance. J. Plant Res. 125 (3), 351–360.
Uclés, O., Villagarcía, L., Cantón, Y., Domingo, F., 2015. Partitioning of non rainfall water input regulated by soil cover type. Catena 139, 265–270.
Veste, M., Littmann, T., 2006. Dewfall and its geo-ecological implication for biological surface crusts in desert sand dunes (north-western Negev, Israel). J. Arid Land Stud. 16 (3), 139–147.
Veste, M., Littmann, T., Friedrich, H., Breckle, S.W., 2001. Microclimatic boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel. Flora 196 (6), 465–474.
Wang, X.P., Pan, Y.X., Hu, R., Zhang, Y.F., Zhang, H., 2014. Condensation of water vapour on moss-dominated biological soil crust, NW China. J. Earth Syst. Sci. 123 (2), 297–305.
Westbeld, A., Klemm, O., Griessbaum, F., Strater, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert. Ann. Geophys. 27 (9), 3571–3576.
Wilske, B., Burgheimer, J., Karnieli, A., Zaady, E., Andreae, M.O., Yakir, D., Kesselmeier, J., 2008. The CO_2 exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev desert, Israel. Biogeosciences 5 (5), 1411–1423.
Wilske, B., Burgheimer, J., Maseyk, K., Karnieli, A., Zaady, E., Andreae, M.O., Yakir, D., Kesselmeier, J., 2009. Modeling the variability in annual carbon fluxes related to biological soil crusts in a Mediterranean shrubland. Biogeosciences 6 (4), 7295–7324.
Wu, L., Lan, S.B., Zhang, D.L., Hu, C.X., 2011. The structure and small-scale vertical distribution of the algae in lichen soil crusts. Microbial. Ecol. 62, 715–724.
Wu, L., Zhang, G.K., Lan, S.B., Zhang, D.L., Hu, C.X., 2013a. Microstructures and photosynthetic diurnal changes in the different types of lichen soil crusts. Eur. J. Soil Biol. 59, 48–53.
Wu, Y.W., Rao, B.Q., Wu, P.P., Liu, Y.D., Li, G.B., Li, D.H., 2013b. Development of artificially induced biological soil crusts in fields and their effects on top soil. Plant Soil 370, 115–124.
Xiao, B., Zhao, Y.G., Wang, Q.H., Li, C., 2015. Development of artificial moss-dominated biological soil crusts and their effects on runoff and soil water content in a semi-arid environment. J. Arid Environ. 117, 75–83.
Zaady, E., Kuhn, U., Wilske, B., Sandoval-Soto, L., Kesselmeier, J., 2000. Patterns of CO_2

exchange in biological soil crusts of successional age. Soil Biol. Biochem. 32 (7), 959–966.

Zhang, J., Zhang, Y.M., Downing, A., Cheng, J.H., Zhou, X.B., Zhang, B.C., 2009. The influence of biological soil crusts on dew deposition in Gurbantunggut Desert, Northwestern China. J. Hydrol. 379 (3), 220–228.

Zhao, Y.G., Bowker, M.A., Zhang, Y.M., Zaady, E., 2016. Enhanced recovery of biological soil crusts after disturbance. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: an Organizing Principle in Drylands. Springer-Verlag, Berlin, Germany, pp. 499–523.

Zheng, Y.P., Xu, M., Zhao, J.C., Bei, S.Q., Hao, L.H., 2011. Effects of inoculated Microcoleus aginatus on the structure and function of biological soil crusts of desert. Biol. Fertil. Soils 47, 473–480.

Zhuang, Y.L., Zhao, W.Z., 2014. Dew variability in three habitats of a sand dune transect in a desert oasis ecotone, Northwestern China. Hydrol. Process. 28 (3), 1399–1408.